WINTER SURVIVAL OF ADULT FEMALE HARLEQUIN DUCKS IN RELATION TO HISTORY OF CONTAMINATION BY THE *EXXON VALDEZ* OIL SPILL

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Abstract: Harlequin duck (*Histrionicus histrionicus*) life-history characteristics make their populations particularly vulnerable to perturbations during nonbreeding periods. The 1989 *Exxon Valdez* oil spill was a major perturbation to nonbreeding habitats of harlequin ducks in Prince William Sound, Alaska, which resulted in population injury. To assess the status of population recovery from the oil spill and to evaluate factors potentially constraining full recovery, we used radiotelemetry to examine survival of adult female harlequin ducks during winters of 1995–96, 1996–97, and 1997–98. We implanted 294 harlequin ducks (154 and 140 in oiled and unoiled areas, respectively) with transmitters and tracked their signals from aircraft during October through March. We examined variation in survival rates relative to area and season (early, mid, and late winter) through comparisons of models using Akaike's information criterion (AIC_c) values. The 3 models best supported by the data indicated that survival of birds in oiled areas was lower than in unoiled areas. Inclusion of standardized body mass during wing molt in the 3 best models did not improve their fit, indicating that body mass during wing molt did not affect subsequent winter survival. In the model that best fit our data, survival was high in early winter for both areas, lower during mid and late winter seasons, and lowest in oiled areas during mid winter. Cumulative winter survival estimated from this model was 78.0% (SE = 3.3%) in oiled areas and 83.7% (SE = 2.9%) in unoiled areas. We determined that area differences in survival were more likely related to oiling history than intrinsic geographic differences. Based on a demographic model, area differences in survival offer a likely mechanism for observed declines in populations on oiled areas. Concurrent studies indicated that harlequin ducks continued to be exposed to residual *Exxon Valdez* oil as much as 9 years after the spill. We suggest that oil exposure, mortality, and population dynamics were linked and conclude that continued effects of the oil spill likely restricted recovery of harlequin duck populations through at least 1998.

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Harlequin ducks spend most of their annual cycle in nearshore marine environments, with breeding age birds leaving only for a few summer months to nest and raise broods on fast-moving streams (Robertson and Goudie 1999). Populations of harlequin ducks may be particularly sensitive to perturbations to their nonbreeding habitats. Harlequin ducks, like many sea ducks, exhibit a life history in which variable and generally low annual reproductive effort is compensated by relatively high adult survival and long reproductive life spans (Goudie et al. 1994). This type of life history would be expected to evolve under conditions of predictable and stable nonbreeding environments (Stearns 1992). Further, Goudie and Ankney (1986) described harlequin ducks, which are small-bodied relative to most other sea ducks, as existing near an energetic threshold during winter, with little flexibility for increasing caloric intake or relying on stored reserves. While this strategy may be tenable under predictable and stable conditions, it does not accommodate perturbations that result in either decreases in energy acquisition or increases in metabolic costs.

The release of nearly 42 million liters of crude oil into the waters of Prince William Sound as a result of the March 1989 grounding of the *Exxon Valdez* was a significant perturbation to the nonbreeding habitat of harlequin ducks. As much as 40% of the spilled oil was deposited in intertidal and subtidal zones of Prince William Sound (Galt et al. 1991, Wolfe et al. 1994), the habitats used by harlequin

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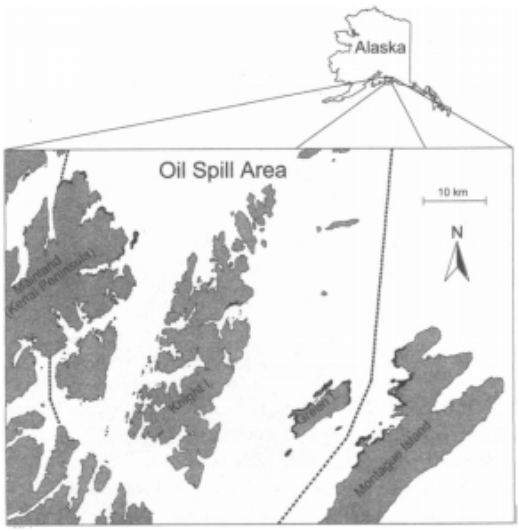

Fig. 1. Study sites for estimating survival of adult female harlequin ducks in Prince William Sound, Alaska. Shorelines in bold represent capture areas. The oil spill area is bounded by dashed lines.

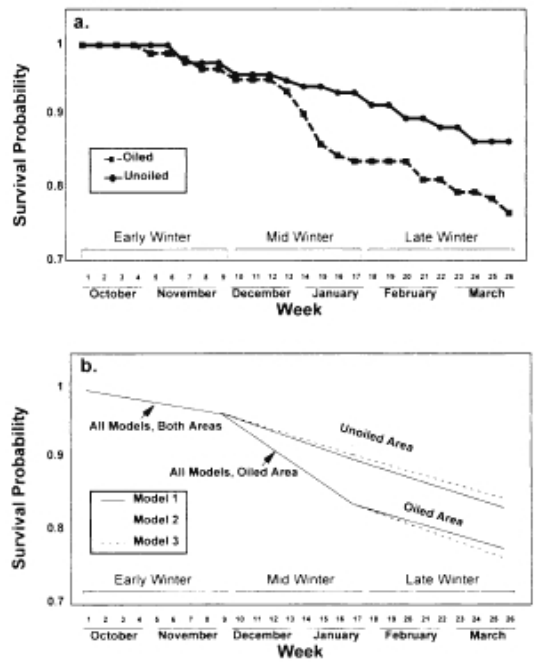

Fig. 2. Winter survival probabilities for harlequin ducks in Prince William Sound, Alaska, based on (a) Kaplan-Meier estimates and (b) the 3 best-fitting reduced models (see Table 1).

ducks, and some residual oil was still present in these areas during our study (Hayes and Michel 1999). Immediate bird mortality from the *Exxon Valdez* oil spill was high (Piatt et al. 1990) and more than 1,000 harlequin ducks were estimated to have died as a direct result of the spill (J. Piatt, U.S. Geological Survey, personal communication). Further, there are concerns that there may be continued, longer-term effects on harlequin duck populations in oil spill-affected areas (Holland-Bartels 2000).

This study was part of a program to assess population recovery of harlequin ducks from the *Exxon Valdez* oil spill in Prince William Sound. We focused on adult female survival during winter because (1) population dynamics of long-lived waterfowl species are particularly sensitive to changes in adult female survival (Goudie et al. 1994, Schmutz et al. 1997), (2) harlequin duck populations are likely sensitive to perturbations on wintering areas, and (3) Prince William Sound is used primarily by harlequin ducks during nonbreeding life stages. Paine et al. (1996), in a critique of studies immediately following the *Exxon Valdez* oil spill, recommended that demographic measures likely provide a better assessment of injury than species occurrence or abundance. We agree, and suggest that demographic studies not only serve to assess injury or recovery status, but also can lend insight into the processes and mechanisms underlying any constraints to full recovery.

METHODS

As described by Paine et al. (1996), the *Exxon Valdez* oil spill was an imperfect experiment—a one-time perturbation without replication and, as in the case of wintering harlequin ducks, with little prespill data for comparison. Under these conditions, our approach was to compare oiled and unoiled areas, while attempting to minimize or account for differences between areas that might confound interpretation of oil spill effects (Wiens and Parker 1995). We recognize that our statistical inference is to areas only, and that assessment of oil spill effects is subject to interpretation. We present ancillary data relevant to this interpretation.

Data Collection

This study was conducted in Prince William Sound (60°N, 148°W), the area most affected by the oil spill, during winters of 1995–96, 1996–97, and 1997–98. We used radiotelemetry to estimate survival of adult female harlequin ducks captured throughout the oil spill zone and on nearby unoiled Montague Island (Fig. 1).

Harlequin ducks, unlike most waterfowl, un-

dergo wing molt on their marine wintering areas (Robertson and Goudie 1999). We herded flocks of flightless birds into funnel traps using sea kayaks during 20 August to 17 September, 1995–97, the dates of peak wing molt by adult females. Captured harlequin ducks were removed from the trap, placed in holding pens, and transported by skiff to a larger vessel for processing. All birds were banded with unique U.S. Fish and Wildlife Service aluminum bands. We identified sex based on plumage characteristics and estimated age class by probing bursal depth (Mather and Esler 1999). Body mass (±1 g) was measured on an electronic balance.

Radiotransmitters were implanted surgically into adult (after third year) female harlequin ducks using modifications (Mulcahy and Esler 1999) of the procedure described by Korschgen et al. (1996). Surgeries were conducted by veterinarians experienced in avian implant procedures. Implanted transmitters have been used successfully in waterfowl studies (Olsen et al. 1992, Haramis et al. 1993), and an increasing body of literature suggests that radiotransmitters implanted into wild waterfowl are less disruptive than external methods of attachment (Esler et al. 2000). Transmitters weighed ≤17.5 g (<3% of average body mass of adult females during wing molt) and had external antennas (Mulcahy and Esler 1999). Birds recovered from anesthesia for at least 1 hr before being released at their capture sites.

Radiomarked harlequin ducks were monitored approximately weekly from an airplane to determine mortality status and location. Monitoring flights began after the first birds were radioed and continued through the last week of March. Transmitters were equipped with mortality sensors that indicated death of a bird by doubling the transmitter pulse rate. Indicated mortalities were confirmed either by recovery of the radio or location of the radiosignal in upland habitats, which harlequin ducks do not use during the nonbreeding season. When radiosignals were lost, monitoring continued until the end of March.

Data Analysis

Unbiased survival estimation using telemetry requires that several critical assumptions are met (Pollock et al. 1989*a*, Tsai et al. 1999), including (1) radioed animals are representative of the population of interest, (2) survival is independent among individuals, (3) radiomarking does not affect survival during the study period, and (4) censoring of animals for which signals are lost is independent of the fate of those animals (i.e., missing animals are no more or less likely to be dead than animals for which fate is known). We felt that the first 2 assumptions were met based on our capture technique and marking regime. We perceived little chance of a systematically biased sample based on susceptibility to capture, as we often were able to catch most birds within a given shoreline segment. Also, because we were marking only adult females, we felt that survival among individuals was independent beyond shared area effects (e.g., we were not marking both members of a pair or a mother and her offspring). We explicitly tested assumptions 3 and 4 (Esler et al. 2000) and found that these were met for our sample.

For each week's sample of relocations, we counted mortalities and numbers of harlequin ducks at risk of mortality (i.e., numbers of detected radios), following procedures outlined in Pollock et al. (1989*a*,*b*) and Bunck et al. (1995). We used 1 October as the beginning of the data analysis period to ensure that all birds in the sample had survived a 14-day post-surgery censor period (Mulcahy and Esler 1999) and had completed wing molt. We made an a priori decision to combine data from all years to assure adequate power for detecting biologically meaningful differences between areas. A small number of birds (n = 6) moved between oiled and unoiled areas during winter; if a bird was detected in a different area for ≥2 consecutive observations, we included those observations in the at-risk data set for the newly occupied area.

We defined seasons as early winter, mid-winter, and late winter, corresponding to the first 9 weeks of data collection, the middle 8 weeks, and the final 9 weeks. Our most general survival model contained 52 parameters (i.e., 1 for each area and week) and corresponded to the Kaplan-Meier method (Pollock et al. 1989*a*) of computing binomial estimates of survival. Variance estimates for this model were calculated using Greenwood's formula (Pollock 1989*a*). We examined the effects of season, area, and several season by area interactions on survival by comparing a series of reduced (fewer parameters) models, in which survival was constrained to be constant among weeks within each season and area combination. We based our inference on the model or models that best fit our data,

Table 1. Models used to estimate winter survival rates of adult female harlequin ducks in Prince William Sound, Alaska, using various combinations of season (early, mid, and late winter) and area (oiled and unoiled). The best model is that with the lowest Akaike information criterion, adjusted for small sample size (AIC_c; Burnham and Anderson 1998). Support for each model is indicated by differences in AIC_c values, not their absolute magnitude; therefore, we present AIC_c values as differences from the best model (Δ AIC_c).

Models	Model description[a]	Number of parameters in model	AIC_c weight	ΔAIC_c
1	EWO = EWU, MWO, MWU = LWO = LWU; survival differs between early winter and other seasons, areas differ during mid-winter	3	0.314	0.0
2	EWO = EWU, MWO, MWU, LWO = LWU; survival differs among all seasons, areas differ during mid-winter	4	0.199	1.0
3	EWO = EWU, MWO, MWU = LWU, LWO; survival differs between early winter and other seasons, areas differ during mid and late winter	4	0.144	1.6
4	EWO = EWU = MWU = LWU, MWO, LWO; survival does not vary seasonally in unoiled areas, areas differ during mid and late winter	3	0.100	2.3
5	EWO = EWU = MWU = LWO = LWU, MWO; survival differs between mid-winter on oiled areas and all other season and area combinations	2	0.088	2.6
6	EW, MW, LW, O()U; survival differs among seasons, with a constant area difference	4	0.074	2.9
7	EWO = EWU, MWO = MWU, LWO = LWU; survival differs by seasons, with no area differences	3	0.046	3.9
8	EWO, EWU, MWO, MWU, LWO, LWU; survival differs by all season and area combinations	6	0.028	4.9
9	EWO = MWO = LWO, EWU = MWU = LWU; survival differs between areas, with no seasonal differences	2	0.004	8.6
10	EWO = EWU = MWO = MWU = LWO = LWU; survival does not vary by season or area	1	0.003	9.4
11	General model; estimates generated for each week and area	52	0.000	35.4

[a] EWO = early winter in oiled areas, EWU = early winter in unoiled areas, MWO = mid-winter in oiled areas, MWU = midwinter in unoiled areas, LWO = late winter in oiled areas, and LWU = late winter in unoiled areas.

Table 2. Parameter estimates (SE) for the top 3 models describing adult female harlequin duck survival during winter in Prince William Sound, Alaska. See Table 1 for model descriptions.

Season[a]	Oiled areas	Unoiled areas
Model 1		
Early winter	0.969 (0.012)	0.969 (0.012)
Mid-winter	0.870 (0.031)	0.934 (0.014)
Late winter	0.925 (0.016)	0.925 (0.016)
Overall	0.780 (0.033)	0.837 (0.029)
Model 2		
Early winter	0.969 (0.012)	0.969 (0.012)
Mid-winter	0.870 (0.031)	0.953 (0.020)
Late winter	0.914 (0.021)	0.914 (0.021)
Overall	0.770 (0.034)	0.843 (0.029)
Model 3		
Early winter	0.969 (0.012)	0.969 (0.012)
Mid-winter	0.870 (0.031)	0.940 (0.017)
Late winter	0.910 (0.030)	0.933 (0.019)
Overall	0.767 (0.039)	0.850 (0.034)

[a] Seasons are of differing lengths (early = 9 weeks, mid = 8 weeks, and late = 9 weeks).

as determined by comparisons of AIC_c values (Burnham and Anderson 1998). The AIC_c indicates the most parsimonious model by balancing the goodness-of-fit of each model (from the maximum likelihood) with the number of parameters to be estimated. Under this approach, the model with the lowest AIC_c indicates the parameters that are supported by the data, which we interpreted as factors related to variation in survival. Models with AIC_c values within 2 units of the AIC_c of the best-fitting model are substantially supported by the data (Burnham and Anderson 1998), and thus we also considered the inference from those models. We also calculated AIC_c weights for each model, which is the weight of evidence that the model is the best of the models considered, given the data. The AIC_c weights for a collection of models sum to 1 and can be used to contrast relative support for each model, and hence the support for the model inference. Survival estimates and variances were calculated by iterative solution of the likelihood using program MARK (White and Burnham 1999). Use of AIC_c to direct model selection and inference deviates from traditional analyses based on significance testing, but is supported by a growing body of literature describing the pitfalls of statistical hypothesis tests (Johnson 1999), particularly for observational studies.

We also assessed whether body mass during wing molt affected subsequent survival by adding standardized body mass to the best-fitting models as determined above. A reduction in AIC_c value would indicate that the addition of the body mass term resulted in a more parsimonious model and that body mass during wing molt was related to winter survival. Body mass was standardized to account for annual, geographic, and molt-stage variation unrelated to our hypothesis of interest by using residuals around a general linear model (Esler et al. 2000) as the body mass parameter. Body mass residuals could not be calculated for 12 of the radioed birds, which were excluded from this analysis.

RESULTS

On 1 October, the beginning of the survival monitoring period, 294 radiomarked adult female harlequin ducks were included in the sample (154 at oiled areas and 140 at unoiled areas). Kaplan-Meier estimates of cumulative winter survival were 76.6 ± 4.0% in oiled areas and 86.6 ± 3.2% in unoiled areas (Fig. 2A).

We contrasted 11 different models with various area and season combinations (Table 1). In the best-fitting model (Model 1), survival varied by season and area, with estimates higher in early winter than other seasons and lower in oiled than unoiled areas during mid-winter (Table 2). Cumulative winter survival estimated from this model was 78.0 ± 3.3% in oiled areas and 83.7 ± 2.9% in unoiled areas. Two other models (Models 2 and 3; Table 1) had AIC_c values <2 units higher than Model 1. In Model 2, survival varied by season and was lower in oiled areas than unoiled during mid-winter (Table 2). In Model 3, survival was high in the fall for both areas, lower and constant during mid and late winter on the unoiled area, and lower on oiled areas than unoiled during mid and late winter, particularly during mid-winter (Table 2). These 3 best models all included an area effect, with survival on oiled areas lower than on unoiled areas (Fig. 2B). The sum of AIC_c weights for models without an area effect was <0.05, indicating that area effects were strongly supported by the data. Similarly, seasonal effects were well supported by the data, with survival during early winter consistently higher than in mid and late winter in the 3 best models. Inclusion of standardized body mass increased AIC_c values of Models 1, 2, and 3 (change in AIC_c ≥0.69), indicating that mass during wing molt was not strongly related to subsequent winter survival.

A difficulty inherent in our study design was

determining whether survival differences between oiled and unoiled areas were more likely related to intrinsic differences (such as habitat, disease, climate, or predator densities) rather than history of oil contamination. To address this, we looked more closely at data for birds (n = 75) from the Green Island area. Although Green Island was in the oil spill area, it was closer to unoiled Montague Island than to other oiled sites (Fig. 1). Also, habitats and harlequin duck densities (D. Esler, unpublished data) were similar to the Montague Island study area. We found that the Kaplan-Meier estimate of cumulative survival of birds captured at Green Island (76.8 ± 5.7% was more similar to that for all oiled areas combined than to unoiled Montague Island. We also contrasted a general season by area model (modified Model 8, Table 1; 3 areas = Green Island, other oiled areas, and unoiled Montague Island) to 2 models each with 2 areas (1 model with Green Island pooled with other oiled areas and 1 model with Green Island pooled with Montague Island). The AIC_c for the model with Green Island pooled with other oiled areas was ≥3.94 units lower than either of the other 2 models, suggesting that oiling history better explains differences in survival between areas than do intrinsic area differences.

DISCUSSION

Winter survival of adult female harlequin ducks was lower on oiled areas than unoiled areas, primarily due to poorer survival on oiled areas during the mid-winter period. In both areas, survival during early winter was higher than during mid or late winter. To understand how these estimates of survival might influence population dynamics, we incorporated the overall cumulative winter survival estimates for each area from Model 1 into a harlequin duck population model (Robertson 1997), holding all other parameters constant. The estimate of annual population change (λ) was 0.9464 for oiled areas (i.e., annual population declines of about 5.4%). For unoiled areas, λ was 1.0054, suggesting a relatively stable population. These estimates are consistent with trends estimated from population surveys conducted during fall 1995–97 (Rosenberg and Petrula 1998). Differences in adult female survival offer a likely mechanism for differences in population trends between areas, and further poor survival on oiled areas may be responsible for population declines.

Our data suggest that area differences in winter survival are more likely due to history of oil contamination than intrinsic area differences. For oiling history to affect survival probabilities and subsequent population trends, there must be some mechanism by which birds from oiled areas are compromised. One potential mechanism is that the immediate effects of the spill or subsequent effects of residual oil resulted in reductions of prey populations. However, during the period of this study, density and abundance of prey were similar between oiled Knight Island and unoiled Montague Island (Holland-Bartels 2000) and winter body mass of female harlequin ducks was similar between oiled and unoiled areas (Holland-Bartels 2000). This suggested that differential food abundance was not responsible for differences in survival between areas.

Exposure to residual *Exxon Valdez* oil is another potential mechanism by which harlequin duck survival could be affected, as oil exposure is known to have deleterious toxic (Leighton 1993) and metabolic (Jenssen 1994) consequences. To determine if harlequin ducks in Prince William Sound were still being exposed to residual oil, Trust et al. (2000) measured induction of cytochrome P4501A (P450), which can indicate exposure to polycyclic aromatic hydrocarbon constituents of crude oil, in harlequin ducks captured during winter 1998 in both oiled and unoiled areas. Cytochrome P450 induction was much higher in harlequin ducks from oiled areas than those from unoiled areas, and Trust et al. (2000) concluded that this was almost certainly due to exposure to residual *Exxon Valdez* oil, because background hydrocarbon levels were negligible in intertidal areas of Prince William Sound prior to the oil spill (Short and Babcock 1996) and polychlorinated biphenyl (PCB) levels were low and similar between areas (Trust et al. 2000). Further, some residual oil was documented in nearshore habitats contemporary with our study (Hayes and Michel 1999). Finally, P450 results from harlequin ducks are consistent with those from several other nearshore vertebrates from oiled areas (B. Ballachey, U.S. Geological Survey, unpublished data).

Could exposure to residual *Exxon Valdez* oil result in lower survival and concomitant population declines? Most lab studies have shown

that mallards (*Anas platyrhynchos*) are tolerant of ingestion of oil, with acute toxic effects not evident until very high doses. These studies have been used to suggest that harlequin ducks should be unaffected by residual *Exxon Valdez* oil (Stubblefield et al. 1995, Boehm et al. 1996). However, other studies have found that the addition of other stressors such as cold temperatures caused oiled ducks in the lab to suffer considerably higher mortality than unoiled birds (Holmes et al. 1978, 1979). This compounding effect of environmental stress and oil exposure seems to be a more appropriate analog for wild harlequin ducks, which exist under relatively harsh winter conditions with little flexibility for accommodating additive stresses (Goudie and Ankney 1986). Our data indicate that mid and late winter may be stressful periods in the annual cycle of harlequin ducks even under unperturbed conditions, as survival on unoiled areas was lower during these seasons than during early winter.

The divergence of survival probabilities between oiled and unoiled areas during mid-winter (Fig. 2) is consistent with a hypothesis of additive effects of oil in the presence of other stressors. Harlequin ducks are visual foragers, and during mid-winter when day length is shortest, they spend most of their time feeding (Goudie and Ankney 1986, Fischer 1998). Prince William Sound is one of the farthest north-wintering areas for harlequin ducks (Robertson and Goudie 1999), thus daylight available for foraging may be particularly limited. Because harlequin ducks have little flexibility for meeting increased energy demands during winter (Goudie and Ankney 1986), which could result from either ingestion of hydrocarbons or plumage oiling (Jenssen 1994), they may be unable to accomodate additive effects of the oil spill, even if relatively small. We speculate that differences in survival and population trends are related to documented differences in contaminant exposure (Trust et al. 2000).

MANAGEMENT IMPLICATIONS

Although populations of some animals may be unaffected or recover rapidly from oil spill effects (Bowman et al. 1995, 1997; Wiens et al. 1996), others such as harlequin ducks have characteristics that make them vulnerable to population-level effects of oil spills for years following the event. For harlequin ducks, these characteristics include a life history requiring high adult survival, occurrence in habitats most affected by oil spills (and which may hold residual oil for years), adaptation to stable and predictable marine environments, and high site fidelity. These traits also make harlequin ducks, and similar species, vulnerable to chronic, low-level oil pollution (Clark 1984). In the cases of either oil spills or chronic oil pollution, the primary management recommendation is, of course, prevention; oil that does not go into the water does not threaten marine bird populations. Unfortunately for harlequin ducks in the spill-affected area, there is little direct management action that now can improve winter survival. Hunter harvest of harlequin ducks is negligible in Prince William Sound and bag limits already were reduced following the oil spill. The extent of the *Exxon Valdez* oil spill zone is too large to recommend intensive habitat restoration; also, residual oil may be deeply buried in sediment (Hayes and Michel 1999) and oil removal efforts could result in significant disruption of intertidal habitats. Therefore, recovery of harlequin duck populations in Prince William Sound will depend largely on natural dispersal and degradation of residual oil and intrinsic population growth.

Wintering aggregations of harlequin ducks are demographically distinct at a relatively fine scale (Cooke et al. 2000). Winter site fidelity of harlequin ducks is high to specific stretches of coastline (Robertson 1997, Cooke et al. 2000) and pair formation occurs on the wintering areas (Gowans et al. 1997, Robertson et al. 1998). Thus, factors that affect survival rates on marine areas can have disproportionate and cumulative effects on these local subpopulations. Fortunately in the case of the *Exxon Valdez* oil spill, levels of dispersal are high enough that subpopulations within the northern Gulf of Alaska were not genetically distinct (Lanctot et al. 1999); the oil spill did not threaten a unique, evolutionarily significant unit (Moritz et al. 1995). However, dispersal rates likely are low, and because of demographic isolation, recovery of groups of birds in oiled areas must occur primarily through recruitment specific to that group (i.e., numbers are not enhanced through immigration from other areas). Population recovery will require not only time for demographic processes to operate, but also elimination of continuing deleterious oil spill effects. Our data suggest that deleterious effects of the *Exxon Valdez* oil spill were evident as many as

9 years following the spill. Managers must recognize that, while oil spill effects may be short-lived for some species, full population recovery for species like harlequin ducks may require decades. In a broader context, the characteristics of harlequin ducks that make them vulnerable to oil spill effects also make them susceptible to population level consequences of other perturbations during nonbreeding periods, including human disturbance, habitat deterioration, and local overharvest.

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